

Identity, Abundance, and Phenology of *Anagrus* spp. (Hymenoptera: Mymaridae) and Leafhoppers (Homoptera: Cicadellidae) Associated with Grape, Blackberry, and Wild Rose in Washington State

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ABSTRACT In 2001 and 2002, we monitored densities of western grape leafhopper, *Erythroneura elegantula* Osborn, and Virginia creeper leafhopper, *Erythroneura ziczac* Walsh (Homoptera: Cicadellidae), eggs from June through September in managed and nonmanaged vineyards in Washington state. *Anagrus* parasitoids (Hymenoptera: Mymaridae) were reared from sampled parasitized leafhopper eggs. Densities of nonparasitized and parasitized *E. elegantula* eggs, and nonparasitized *E. ziczac* eggs, were significantly higher in nonmanaged grapevines, although this pattern was not consistent for the latter two groups. Densities of parasitized *E. ziczac* eggs were consistently low across management regimes. *Anagrus erythroneurae* S. Trjapitzin & Chiappini, *Anagrus daanei* S. Triapitsyn, and *Anagrus tretiakovae* S. Triapitsyn emerged from parasitized *E. elegantula* eggs, whereas latter two mymarid species also parasitized *E. ziczac* eggs. Of these species, *A. tretiakovae* was the most common parasitoid of *Erythroneura* leafhopper eggs within sampled vineyards. From 2001–2003, we used yellow sticky traps to collect *Anagrus* wasps and potential leafhopper hosts from blackberry, grape, and wild rose sites, because these habitats might serve as refugia for the wasps. All three *Anagrus* species collected within vineyards and a fourth species, *A. atomus* L., were found on traps in these plant habitats. Several leafhopper taxa that could serve as potential alternative hosts for *Anagrus* spp. also were collected. Our collection of *A. daanei*, *A. tretiakovae*, and *A. atomus* in Washington represents range extensions for these species, revealing several novel candidate species for conservation. Because we consistently found *Anagrus* species of agricultural importance within rose and blackberry patches, cultivation of these plants close to vineyards may enhance colonization by *Anagrus* and thus improve grape leafhopper biocontrol.

KEY WORDS *Anagrus*, *Erythroneura*, leafhoppers, grape, blackberry

The western grape leafhopper, *Erythroneura elegantula* Osborn, and the Virginia creeper leafhopper, *Erythroneura ziczac* Walsh (Homoptera: Cicadellidae), are the primary leafhopper pests in south central Washington state vineyards (Cone et al. 1990, Olsen et al. 1998, Wright et al. 1998, James et al. 2002). Nymphal and adult leafhoppers damage grape leaves by ingesting leaf cell contents, causing a reduction in photosynthesis (Jensen and Flaherty 1981), vine vigor, and berry sugar content (McKenzie and Beirne 1972, Olsen et al. 1998). The eggs of both leafhopper species are laid beneath the leaf epidermis, primarily on the

leaf underside (Olsen and Cone 1997). *E. elegantula* eggs are laid singly across the leaf surface (Olsen and Cone 1997) and are slightly curved. In contrast, *E. ziczac* eggs are usually laid in groups of two or more, although they are sometimes laid singly (Cate 1975, Olsen 1995, Olsen and Cone 1997) and they are covered with brochosomes, which are net-like spheres that may repel other leafhoppers and/or deter parasitism (Olsen 1995, Velema et al. 2005). Thus, eggs of the two leafhopper species are distinguishable.

Several natural enemies attack *Erythroneura* leafhoppers, including mymarid egg parasitoids in the genus *Anagrus* (McKenzie and Beirne 1972, Cate 1975, Williams 1984, Triapitsyn 1998, Martinson et al. 2001). Historically, parasitism of grape leafhopper eggs in the United States (e.g., Douth and Nakata 1973, Wells and Cone 1989, Triapitsyn 1998) and Canada (McKenzie and Beirne 1972) has been attributed to *Anagrus epos* Girault. In California life table studies, *A. epos* was the most important factor regulating populations of *E. elegantula* (Cate 1975). In 1998, Triapitsyn reexamined *A. epos* specimens, which were primarily from California and New York, and found that several *Ana-*

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grus species were erroneously identified as *A. epos*. However, Triapitsyn (1998) did not reexamine specimens from Washington; thus, the identity and incidence of *Anagrus* grape leafhopper egg parasitoids in Washington vineyards has remained unclear.

Like other natural enemies, the use of nonselective pesticides can adversely impact *Anagrus* parasitoids (de Courcy Williams and Gill 1996, Martinson et al. 2001). Martinson et al. (2001) found that exposure to carbaryl, methyl parathion, and sulfur residues increased mortality of *Anagrus* adults. In addition, de Courcy Williams and Gill (1996) found that heptenophos and pirimicarb increased mortality of *A. atomus* (L.) larvae within *Empoasca decipiens* Paoli eggs. To counteract *Anagrus* loss due to pesticide application and other disruptive cultural practices, surrounding habitats could be managed to provide refugia and alternative hosts for the wasps (Doutt and Nakata 1965, 1973; Williams 1984; Kido et al. 1984; Wilson et al. 1989; Pickett et al. 1990; Murphy et al. 1996), although it is important to consider the impact of refuge size on *Anagrus* populations and pest biocontrol (Thies and Tscharnitke 1999, Cronin 2004). *Anagrus* spp. overwinter within leafhopper eggs (Mulla 1956, Williams 1984), but *Erythroneura* leafhopper species in grape spend the winter as adults (Cate 1975, Wells and Cone 1989, Cone et al. 1990, Olsen and Cone 1997). Thus, overwintering *Anagrus* require an alternate source of leafhopper eggs (Doutt and Nakata 1965, 1973; Williams 1984; Murphy et al. 1996; Williams and Martinson 2000). *Anagrus* spp. can parasitize eggs of leafhopper species on wild rose (*Rosa* spp.) (McKenzie and Beirne 1972) and blackberry (*Rubus* spp.) (e.g., Doutt and Nakata 1965, Williams 1984), among other plants (Kido et al. 1984, Williams and Martinson 2000) and then migrate from these nearby refuges back into vineyards in the spring (Williams 1984, Corbett and Rosenheim 1996a). Therefore, the presence of surrounding vegetation housing acceptable overwintering hosts can bolster parasitoid densities within adjacent vineyards (Doutt and Nakata 1965, 1973; Murphy et al. 1996, 1998).

However, a first step for Washington state will be to identify resident *Anagrus* species and their overwintering host. This article presents the results of a survey where we identified the *Anagrus* wasps parasitizing *Erythroneura* leafhopper eggs in both managed and nonmanaged grapevines in central Washington. Additionally, we recorded the identity and phenology of *Anagrus* species and potential leafhopper hosts within grape, blackberry, and wild rose patches, as these plants might serve as important refuges for *Anagrus* parasitoids.

Materials and Methods

***Anagrus* and Leafhopper Eggs Collected from Vineyards.** In 2001, *Anagrus* spp. were reared from *Erythroneura* spp. eggs on grape leaves (*Vitis* spp.) collected from 15 managed vineyards and nine nonmanaged grapevine sites. In 2002, *Anagrus* were reared from a subset of 14 managed vineyards and eight non-

managed grapevine sites. In both years, the densities of nonparasitized and parasitized *E. elegantula* and *E. ziczac* eggs also were recorded. Managed grapevines were standard varieties (predominantly Merlot or Cabernet Sauvignon), treated with pesticides, fertilized, irrigated, trellised, and pruned. In contrast, nonmanaged sites were composed of abandoned grapevines, backyard vines managed by home or store-owners, or nonmanaged blocks within managed vineyards. Most grapevine varieties in nonmanaged sites were either unknown, or were atypical of Washington viticulture (e.g., Black Hamburg, Black Prince, and Baco Noir (WASS 2005). Additionally, grapevines at the majority of nonmanaged sites were not exposed to chemicals, were not trellised or pruned, and were rarely irrigated or fertilized.

Sites were located in the following grape-growing regions within south central Washington and northern Oregon: the Columbia River Valley, the Quincy Basin area, the Yakima Valley, and the Walla Walla Valley. Most sites were sampled each month from June to September, although in 2001, two sites (one managed and one nonmanaged) were sampled for only 3 mo due to late discovery. Missing data for these sites were replaced by an average value across each type of management regime on that sample date (von Ende 1993).

During each sampling period, 10 leaves were collected from each corner of a managed vineyard block, whereas in nonmanaged sites 40 leaves were taken haphazardly (Gotelli and Ellison 2004) from throughout the patch, because these plants were not arranged geometrically. Leaves were placed into self-sealing plastic bags, labeled, stored in a cooler ($\approx 15^{\circ}\text{C}$) for transport, and then placed in a refrigerator (8°C). Within 10 d, leaves were examined under a dissecting microscope (45 \times ; Leica MZ6, Leica Microsystems Inc., Buffalo, NY), and leaf squares containing parasitized leafhopper eggs were excised using a scalpel. Parasitized leafhopper eggs were readily separated from nonparasitized eggs because the former develop a light cream-colored spot, which soon turns orange or red (Olsen and Cone 1997). From June to September 2001, and from June to July 2002, a maximum of 20 parasitized eggs were retained per site each month. In August and September 2002, all parasitized eggs were retained due to low parasitism, with eggs deposited in groups of two or more (*E. ziczac*) being separated from eggs laid singly (*E. elegantula*). In 2001 and before August in 2002, we did not separate *E. elegantula* and *E. ziczac* eggs. Leaf tissue containing eggs was placed on moist paper towel circles (3 cm in diameter) inside plastic rearing cups (3-cm in height by 3 cm in diameter). Cup lids were perforated with a pin for ventilation, labeled, and cups were then placed under 40-W incandescent illumination at room temperature ($\approx 25^{\circ}\text{C}$) to allow parasitoids to complete development. Rearing cups remained under illumination up to 3 wk, which is longer than *Anagrus* developmental time from oviposition to adult emergence at that temperature (Chantarasard et al. 1984, Williams 1984, Hesami et al. 2004). *Anagrus* adults that emerged from eggs were removed from the rearing cup by using a

fine paintbrush, placed into Hoyer's solution, and adult females were identified under a compound microscope (Olympus CH, Olympus Optical Co. Ltd., Tokyo, Japan) by using the keys and descriptions in Triapitsyn (1998) and Chiappini et al. (1996). The keys were only for *Anagrus* females, and so males were not identified.

***Anagrus* and Leafhoppers on Sticky Traps.** Yellow sticky traps (23 by 18 cm; Pherocon AM Trécé Inc., Salinas, CA) were used to monitor densities of adult *Anagrus* at blackberry, grape, and wild rose sites from 2001 through 2003. There were five blackberry, five grape, and two wild rose sites, all located within the Yakima Valley, WA, between the cities of Grandview and West Richland. The blackberry sites were wild Himalayan blackberry, *Rubus armeniacus* Focke, which was growing in pastures, riparian, or nonagricultural areas. The grape sites were more varied: one site was a 15-m row of nonsprayed vines at a residence, two sites were nonsprayed blocks on Washington State University-Prosser land, and two sites were commercial vineyard blocks, one block with high pesticide input and the other block nonsprayed. We hung two sticky traps at the top of the canopy at each grape site except for the residence site, which only received a single trap because of the small number of vines at that location. The wild rose sites were in riparian habitats near the Yakima River and consisted of native Wood's rose, *Rosa woodsii* Lindley. The rose and blackberry sites were not sprayed with chemicals, and each site had two sticky traps. Traps at these sites were placed 1.5–2.0 m above the ground and positioned so that they were not obscured by foliage. Traps were collected and replaced weekly from 3 April 2001 until 25 November 2003, with the exception of the period from mid-December to early April in blackberry and rose sites, when traps were collected and replaced twice per month. Grape sites were not monitored during the winter because *Anagrus* spp. do not overwinter on grape (Doutt and Nakata 1965). The density of all *Anagrus* individuals on each trap was recorded from the inner counting grid on each card (area of 22.86 by 17.78 cm), and a subsample of five adult females was removed haphazardly from each trap for identification by scraping the wasps and surrounding sticky material off the traps with a scalpel blade, applying the specimens to microscope slides, and covering them with coverslips. The females were identified to species as described previously. Numbers of adult and nymphal leafhoppers also were recorded and identified using Wolfe (1955) and Hamilton (1985).

Statistics. Densities of *Anagrus* and leafhoppers were log ($x + 1$) transformed before analysis, and time-series data were analyzed using repeated measures multiple analysis of variance (MANOVA) (von Ende 1993) in SYSTAT (SPSS Inc. 1998). If time interactions were not significant, data were combined across sampling dates, and these seasonal means were analyzed using analysis of variance (ANOVA) followed by Tukey's post hoc test. For sticky trap data, year was used as the time factor in repeated measures MANOVA, due

Table 1. Statistical parameters for *Anagrus* reared from leafhopper eggs from vineyards

	Statistical parameters ^{a,b}		
	Wilks' λ	<i>F</i>	<i>P</i>
<i>A. daanei</i>			
Yr	n/a	1.868	0.179
Management	n/a	2.507	0.121
Yr \times management	n/a	3.944	0.054
Time	0.844	2.466	0.076
Time \times yr	0.886	1.711	0.180
Time \times management	0.837	2.606	0.065
Time \times yr \times management	0.858	2.203	0.103
<i>A. erythroneurae</i>			
Yr	n/a	0.056	0.815
Management	n/a	0.429	0.516
Yr \times management	n/a	0.063	0.804
Time	0.974	0.358	0.784
Time \times yr	0.794	3.468	0.025
Time \times management	0.956	0.618	0.607
Time \times yr \times management	0.978	0.294	0.829
<i>A. tretiakovae</i>			
Yr	n/a	0.035	0.853
Management	n/a	0.502	0.483
Yr \times management	n/a	0.369	0.547
Time	0.744	4.576	0.008
Time \times yr	0.996	0.059	0.981
Time \times management	0.860	2.175	0.106
Time \times yr \times management	0.911	1.303	0.287
Males			
Yr	n/a	0.023	0.879
Management	n/a	3.467	0.070
Yr \times management	n/a	0.540	0.467
Time	0.759	4.245	0.011
Time \times yr	0.846	2.421	0.080
Time \times management	0.930	1.009	0.399
Time \times yr \times management	0.857	2.218	0.101

n/a, not applicable.

^a Univariate between subjects analysis: df = 1, 42.

^b Multivariate repeated measures analysis: df = 3, 40.

to the limited number of sample sites for each plant type relative to the number of sample dates.

Results

***Anagrus* Reared from Grapevines.** We identified three species of parasitoids from *Erythroneura* spp. eggs on grapevines: *A. daanei* S. Triapitsyn, *A. erythroneurae* S. Trjapitzin & Chiappini, and *A. tretiakovae* S. Triapitsyn. Although other *Anagrus* females emerged from parasitized eggs, physical damage due to desiccation rendered the specimens unidentifiable. From June to September 2001, and from June through July 2002, individual wasp species could not be positively attributed to emerging from *E. elegantula* or *E. ziczac* eggs, because eggs of the two leafhopper species were not incubated separately during this time period. However, during August and September 2002, *E. elegantula* and *E. ziczac* eggs were separated. During these 2 mo, two *A. daanei*, nine *A. erythroneurae*, 93 *A. tretiakovae*, 39 unknown females, and 109 males emerged from parasitized *E. elegantula* eggs collected from 11 managed and six nonmanaged sites. Also, from August to September 2002, 11 *A. daanei*, one *A. tretiakovae*, four unknown females, and four male specimens emerged from parasitized *E. ziczac* eggs collected from one managed and one nonmanaged site.

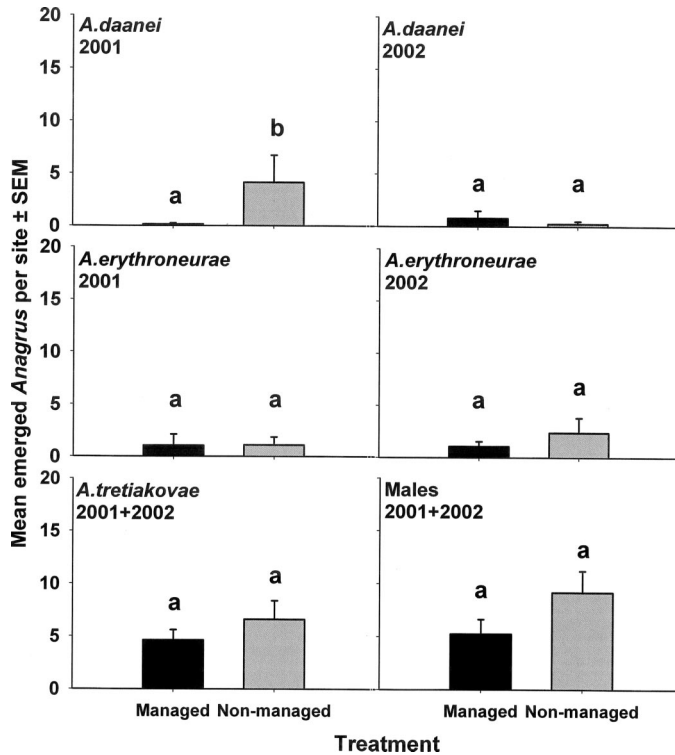


Fig. 1. Total densities of identified adult *Anagrus* species (females only) and *Anagrus* males reared from *Erythroneura* leafhopper eggs collected from managed and nonmanaged vineyard sites. Data are means and standard errors.

Densities of *A. daanei* (identified females only) did not change dramatically during the season, leading to a nonsignificant time effect in repeated measures MANOVA ($P > 0.05$; Table 1). Sampling year had a significant effect on the impact of vineyard management on *A. daanei* densities ($P = 0.054$; Table 1); therefore, we ran separate ANOVAs of seasonal means for each year. In 2001, *A. daanei* densities were significantly higher in nonmanaged sites (management, $F = 5.339$, $P = 0.031$; Fig. 1), whereas in 2002 vineyard management did not impact densities of this parasitoid species (management, $F = 0.107$, $P = 0.747$; Fig. 1). Seasonal changes in *A. erythroneurae* densities (identified females only) differed between years, leading to a significant time \times year interaction ($P = 0.025$; Table 1); thus, we ran separate ANOVAs of seasonal means for each year. In 2001, *A. erythroneurae* densities remained relatively constant (Wilks' $\lambda = 0.713$, $F = 2.683$, $P = 0.074$), whereas in 2002, their densities gradually decreased throughout the season (Wilks' $\lambda = 0.634$, $F = 2.465$, $P = 0.038$). Vineyard management did not have a significant impact on *A. erythroneurae* densities in either year (2001: time \times management, Wilks' $\lambda = 0.924$, $F = 0.550$, $P = 0.654$; management, $F = 0.077$, $P = 0.784$; and 2002: time \times management, Wilks' $\lambda = 0.900$, $F = 0.664$, $P = 0.585$; management, $F = 0.448$, $P = 0.511$) (Fig. 1). Densities of *A. tretiakovae* (iden-

tified females only) and *Anagrus* males increased from June to August in both managed and nonmanaged sites and then rapidly declined in September in the latter sites, leading to a significant time effect in repeated measures MANOVA ($P < 0.05$; Table 1). However, densities of *A. tretiakovae* and *Anagrus* males did not differ significantly due to year, management regime, or due to interactive effects between these variables with one another or with time ($P < 0.05$; Table 1; Fig. 1).

Leafhopper Eggs from Vineyards. Densities of nonparasitized *E. elegantula* fluctuated throughout the season, leading to a significant time effect in repeated measures ANOVA ($P < 0.05$; Table 2). In both managed and nonmanaged sites, densities of nonparasitized *E. elegantula* eggs gradually decreased from June to July, peaked in August, and declined in September. Densities of nonparasitized *E. elegantula* eggs were significantly higher in nonmanaged sites ($P = 0.006$; Table 2; Fig. 2). In 2001, parasitized *E. elegantula* densities increased throughout the season, whereas in 2002 they remained relatively constant, leading to a significant time \times year interaction ($P = 0.019$; Table 2); therefore, we ran separate ANOVAs of seasonal means for each year. In 2001, densities of parasitized *E. elegantula* eggs were significantly higher in nonmanaged sites (time \times management, Wilks' $\lambda = 0.823$, $F = 1.434$, $P = 0.263$; management, $F =$

Table 2. Statistical parameters for leafhopper eggs collected from vineyards

	Statistical parameters ^{a,b}		
	Wilks' λ	F	P
EE nonparasitized			
Yr	n/a	2.222	0.143
Management	n/a	8.395	0.006
Yr \times management	n/a	2.290	0.138
Time	0.579	9.686	<0.001
Time \times yr	0.886	1.712	0.180
Time \times management	0.986	0.183	0.907
Time \times yr \times management	0.927	1.049	0.381
EE parasitized			
Yr	n/a	4.922	0.032
Management	n/a	6.041	0.018
Yr \times management	n/a	5.146	0.029
Time	0.605	8.705	<0.001
Time \times yr	0.783	3.697	0.019
Time \times management	0.945	0.771	0.517
Time \times yr \times management	0.910	1.323	0.280
EZ nonparasitized			
Yr	n/a	0.277	0.601
Management	n/a	10.382	0.002
Yr \times management	n/a	0.122	0.728
Time	0.570	10.064	<0.001
Time \times yr	0.996	0.058	0.982
Time \times management	0.671	6.529	0.001
Time \times yr \times management	0.977	0.309	0.819
EZ parasitized			
Yr	n/a	1.497	0.228
Management	n/a	1.733	0.195
Yr \times management	n/a	1.988	0.166
Time	0.949	0.714	0.550
Time \times yr	0.941	0.833	0.484
Time \times management	0.946	0.754	0.527
Time \times yr \times management	0.957	0.595	0.622

EE, *E. elegantula*; EZ, *E. ziczac*; n/a, not applicable.^a Univariate between subjects analysis: df = 1, 42.^b Multivariate repeated measures analysis: df = 3, 40.

9.024, $P = 0.007$; Table 3; Fig. 2), whereas in 2002, vineyard management did not significantly impact their densities (time \times management, Wilks' $\lambda = 0.984$, $F = 0.098$, $P = 0.960$; management, $F = 0.026$, $P = 0.874$; Table 3; Fig. 2).

In managed vineyards densities of nonparasitized *E. ziczac* eggs peaked in July, whereas in nonmanaged sites densities peaked in June and then gradually declined, leading to a significant time effect in repeated measures MANOVA ($P < 0.05$; Table 2). Vineyard management affected densities of nonparasitized *E. ziczac* eggs in an inconsistent manner throughout the season, leading to a significant time \times management interaction ($P < 0.05$; Table 2; Fig. 2). To further explore this interaction we then conducted separate ANOVAs for each sampling date. In June and August, densities of nonparasitized *E. ziczac* eggs were significantly higher in nonmanaged sites (June, $P = 0.002$; August, $P = 0.002$; Fig. 2), whereas there were no significant impacts of vineyard management on their densities in July ($P = 0.132$) and September ($P = 0.510$, Fig. 2). Densities of parasitized *E. ziczac* eggs were extremely low, and they did not significantly change throughout the season ($P > 0.05$; Table 2).

Vineyard management did not impact densities of parasitized *E. ziczac* eggs ($P > 0.05$; Table 2; Fig. 2).

Anagrus on Sticky Traps. Four species of *Anagrus* were identified from sticky traps associated with blackberry, grape, and wild rose: *Anagrus atomus*, *A. daanei*, *A. erythroneurae*, and *A. tretiakovae*. We also collected several other unidentified *Anagrus* spp. from the *incarnatus* species group. These *Anagrus* could not be identified because the sticky material did not clear the specimens, preventing us from seeing important anatomical features of this group. Based on positively identified specimens that were collected in this region, we think that the unidentified species are likely: *Anagrus oregonensis* S. Triapitsyn, *Anagrus avalae* Soyka, *Anagrus columbi* Perkins, *Anagrus nigricentris* Girault, and/or *Anagrus flaveolus* Waterhouse.

Seasonally, densities of *A. atomus* (identified females only) were highest in all plant types from mid-April to late June, whereas *A. daanei* and *A. tretiakovae* densities (identified females only) peaked in late September (Fig. 3). There were two peaks of *A. erythroneurae* (identified females only) abundance in blackberry and wild rose habitats, one peak beginning in late April and the other peak in August (Fig. 3). However, in grapevines *A. erythroneurae* densities increased gradually from May through November (Fig. 3). On blackberry and rose, densities of *Anagrus* males peaked in late May, whereas on grape their densities peaked in late August (Fig. 3).

In repeated measures analysis, plant type affected the densities of *A. atomus*, *A. daanei*, *A. erythroneurae*, and *A. tretiakovae* in a manner that was consistent between years (year \times plant, $P > 0.05$; Table 3); thus, we combined data from all years. Plant type had a significant impact on *A. atomus* and *A. erythroneurae* densities ($P < 0.05$; Table 3), with densities in blackberry significantly higher than those on grape (*atomus*, $P = 0.040$; *erythroneurae*, $P = 0.023$; Fig. 4). There were no significant differences in *A. atomus* or *A. erythroneurae* densities between blackberry and rose (*atomus*, $P = 0.272$; *erythroneurae*, $P = 0.361$; Fig. 4), or grape and rose (*atomus*, $P = 0.842$; *erythroneurae*, $P = 0.574$, Fig. 4). Additionally, there were no significant differences in total densities of *A. daanei*, *A. tretiakovae*, or all *Anagrus* females ($P > 0.05$; Table 3; Fig. 4). Sampling year did affect densities of *Anagrus* males; thus, data from each year were analyzed separately (year \times plant, $P = 0.006$; Table 3). However, in all 3 yr, there were no significant differences in densities of *Anagrus* males between plant types ($P > 0.05$; Table 3; Fig. 4).

Leafhoppers on Sticky Traps. Six leafhopper taxa were identified from sticky traps associated with blackberry, grape, and wild rose: *Arboridia* sp., *Dikrella* sp., *Empoasca* sp., *Erythroneura elegantula*, *E. ziczac*, and *Edwardsiana rosae* (L.) / *Typhlocyba pomaria* McAtee. *E. rosae* and *T. pomaria* adults are difficult to distinguish (Elsner and Beers 1988); thus, we did not separate these two species.

Seasonally, densities of *Arboridia* in blackberry and rose peaked in mid-March, although their densities increased again in October and November (Fig. 5).

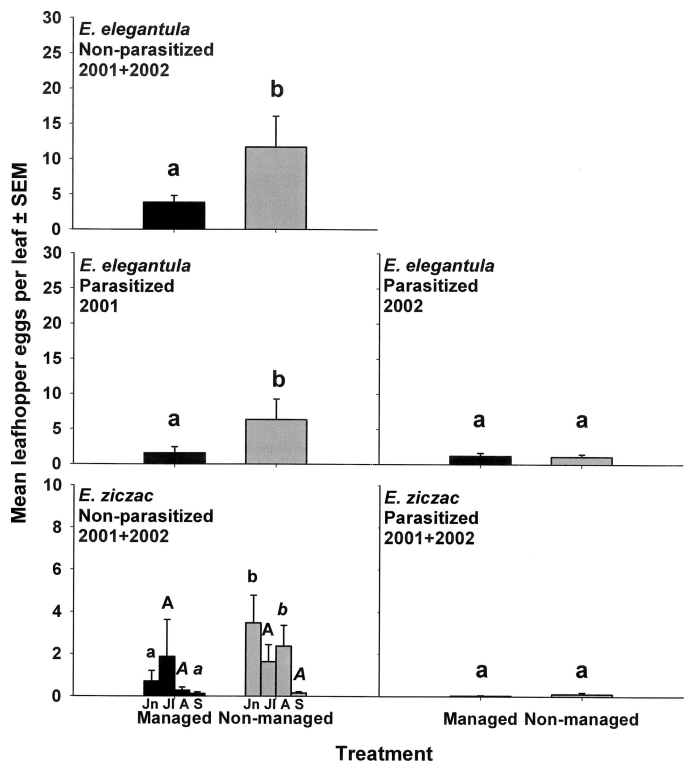


Fig. 2. Total densities of nonparasitized and parasitized *Erythroneura* leafhopper eggs. Data are means and standard errors. Jn, June; Jl, July; A, August; and S, September.

Densities of *Arboridia* from grapevines and *Dikrella* were low throughout the season. In all three habitats, densities of *Empoasca* were highest from late April to

July (Fig. 5). There were two peaks in abundance of *E. elegantula* and *E. ziczac*, one peak in mid-April in blackberry, and one peak from July to October in grape (Fig. 5). In blackberry and rose habitats, densities of *Edwardsiana*/*Typhlocyba* were highest from late September to mid-November, with a smaller peak in late May for blackberry (Fig. 5).

Plant type affected the densities of the five most common leafhopper taxa in a manner that was consistent between years (year \times plant, $P > 0.05$; Table 4); thus, we combined data from all years. Densities of *Arboridia* were significantly lower in grapevines compared with blackberry ($P = 0.050$) and rose plants ($P = 0.008$). There were no significant differences in *Arboridia* densities between blackberry and rose traps ($P = 0.194$; Fig. 6). In contrast, there were no significant differences in *Dikrella*, *E. elegantula*, *E. ziczac*, or *Empoasca* densities between plant types ($P > 0.05$; Table 4; Fig. 6). Sampling year did affect *Edwardsiana*/*Typhlocyba* densities; thus, data from each year were analyzed separately (year \times plant, $P = 0.010$; Table 4). In all 3 yr, *Edwardsiana*/*Typhlocyba* densities were significantly lower in grape habitats than in blackberry (2001, $P = 0.003$; 2002, $P = 0.001$; and 2003, $P = 0.001$) and rose habitats (2001, $P = 0.006$; 2002, $P = 0.041$; and 2003, $P = 0.012$; Fig. 6). There were no significant differences in *Edwardsiana*/*Typhlocyba* densities between the latter two plant types (2001, $P = 0.850$; 2002, $P = 0.429$; and 2003, $P = 0.791$; Fig. 6).

Table 3. Statistical parameters for <i>Anagrus</i> from sticky traps			
	Wilks' λ	F	P
<i>A. atomus</i>			
Plant ^a	n/a	4.499	0.044
Yr ^b	0.121	28.964	<0.001
Yr \times plant ^c	0.351	2.756	0.064
<i>A. daaneii</i>			
Plant ^a	n/a	0.661	0.540
Yr ^b	0.439	5.103	0.037
Yr \times plant ^c	0.560	1.347	0.296
<i>A. erythroneurae</i>			
Plant ^a	n/a	5.407	0.029
Yr ^b	0.640	2.245	0.168
Yr \times plant ^c	0.484	1.747	0.189
<i>A. tretiakovae</i>			
Plant ^a	n/a	2.523	0.135
Yr ^b	0.969	0.130	0.880
Yr \times plant ^c	0.887	0.247	0.908
Males			
Plant ^a			
2001	n/a	1.033	0.395
2002	n/a	2.297	0.156
2003	n/a	0.574	0.583
Yr ^b	0.699	1.723	0.239
Yr \times plant ^c	0.179	5.450	0.006

n/a, not applicable.
^a Univariate between subjects analysis: df = 2, 9.
^b Multivariate repeated measures analysis: df = 2, 8.
^c Multivariate repeated measures analysis: df = 4, 16.

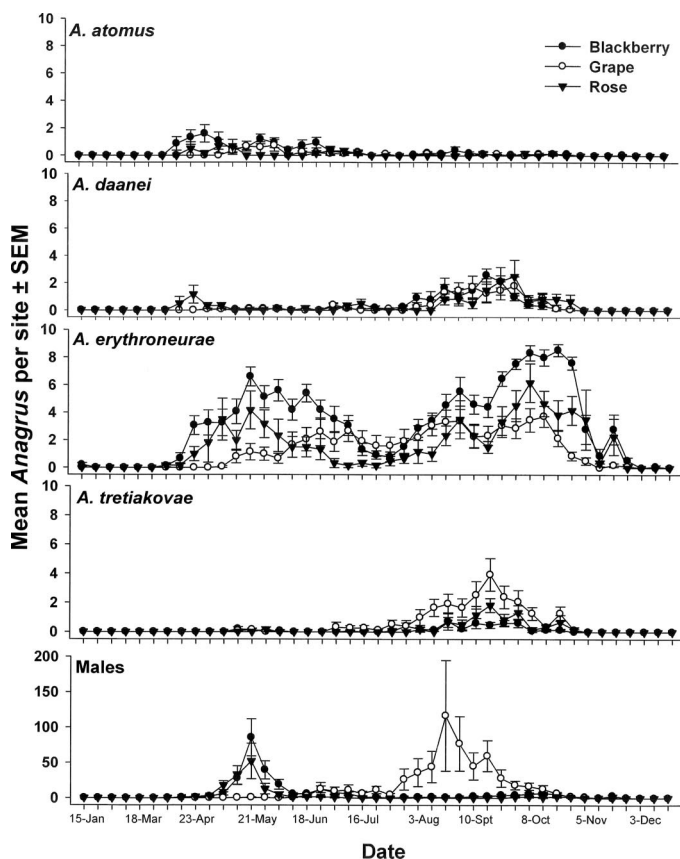


Fig. 3. Seasonal densities of identified adult *Anagrus* species (females only) and *Anagrus* males collected on sticky traps in blackberry, grape, and wild rose habitats. The 2001–2003 data are combined. Data are means and standard errors.

Discussion

Historically, *Anagrus epos* was thought to be the primary mymarid species attacking grape leafhoppers in much of the United States (Wells and Cone 1989, Zimmerman et al. 1996, Triapitsyn 1998) and Canada (McKenzie and Beirne 1972). It was only recently that researchers discovered that several *Anagrus* species erroneously identified as *Anagrus epos* were instead one or several other species (Triapitsyn 1998). Our survey has revealed that this is also the case in Washington state, with our local “*A. epos*” instead being at least three *Anagrus* species (*A. daanei*, *A. tretiakovæ*, and *A. erythroneuræ*). This is a range extension for both *A. daanei* and *A. tretiakovæ*, although *A. erythroneuræ* specimens have previously been collected in Washington from eggs of *T. pomaria* (Triapitsyn 1998). Furthermore, we found that all three *Anagrus* species parasitize *Erythroneura elegantula* eggs and that *A. daanei* and *A. tretiakovæ* also parasitize *E. ziczac* eggs on grapevines. In New York, Williams and Martinson (2000) found a complex of species parasitizing leafhoppers eggs on grapevines (*Vitis vinifera*, *V. labrusca*, and *V. riparia*), including: *A. daanei*, *A. erythroneuræ*, *A. nigriventris*, *A. epos*, and

A. tretiakovæ. The first two species also attack grape leafhoppers in California, whereas the latter two species, along with *A. flaveolus* Waterhouse, are associated with grapevines in Mexico (Triapitsyn 1998).

A. daanei was the most common mymarid reared from *E. ziczac* eggs, and it also was reared from *E. elegantula* eggs. Williams and Martinson (2000) found that this mymarid species parasitized *E. ziczac* eggs in New York, and Triapitsyn (1998) also recorded it as a parasitoid of *E. elegantula* eggs. In our study, parasitism of *E. ziczac* eggs was extremely low, even though densities of nonparasitized *E. ziczac* eggs were only slightly lower than nonparasitized *E. elegantula* eggs. Differences in parasitism rates of *E. elegantula* and *E. variabilis* eggs have been documented in Californian vineyards (Settle and Wilson 1990) because the eggs of the former were laid closer to the leaf surface, making them more susceptible to parasitism (Settle and Wilson 1990). Although differences in parasitism of *E. elegantula* and *E. ziczac* eggs could be related to differences in their egg-laying patterns (laid individually versus in groups), the presence of brochosomes, or net-like spheres that surround *E. ziczac* eggs (Olsen 1995), also may retard parasitism (Velema

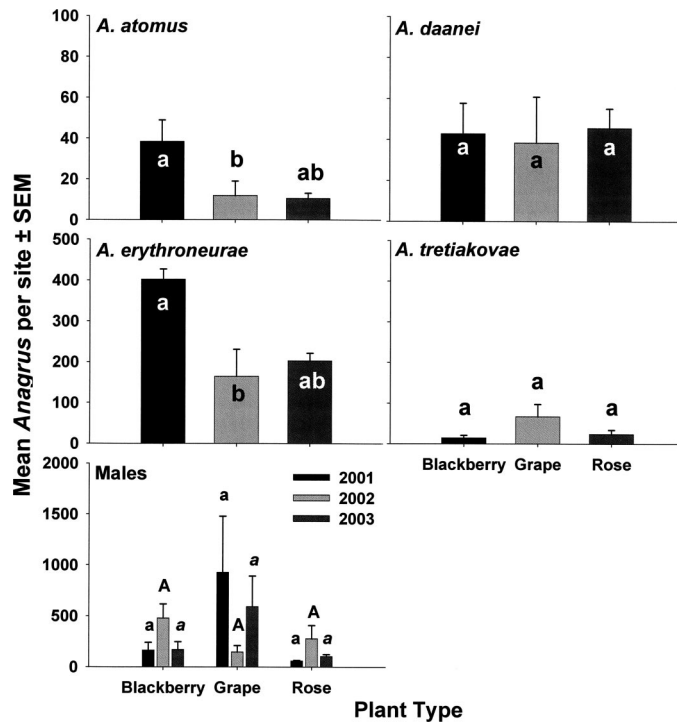


Fig. 4. Total densities of identified adult *Anagrus* species (females only) and *Anagrus* males collected on sticky traps in blackberry, grape, and wild rose habitats. Data are means and standard errors.

et al. 2005). Velema et al. (2005) found that brochosomes produced by the glassy-winged sharpshooter, *Homalodisca coagulata* (Say), reduced parasitism by the mymarid *Gonatocerus ashmeadi* Girault. *A. daanei* may be the best adapted species for exploiting *E. ziczac* as a host; thus, restrictions in the abundance of this mymarid in vineyards would likely result in poor natural regulation of this leafhopper pest. *A. daanei* parasitizes at least 11 species of leafhoppers on almond, apple, blackberry, table and wine grapes, rose, black locust (*Robinia pseudo-acacia* L.), sugar maple (*Acer saccharum* Marsh.), and common prickly ash (*Zanthoxylum americanum* Mill.) (Triapitsyn 1998, Williams and Martinson 2000). *Anagrus daanei* is known to parasitize *E. rosae* (Triapitsyn 1998), and Seyd-oleslami and Croft (1980) found that it frequently attacks *T. pomaria* eggs on apple (*Malus* spp.), although they mistakenly thought the wasps were *A. epos* (Triapitsyn 1998). *Dikrella* leafhoppers on blackberry are also probable hosts (Triapitsyn 1998).

A. erythroneuræ was frequently reared from *Erythroneura* eggs, and several studies indicate the importance of this species as a leafhopper parasitoid in California and New York vineyards (Trjapitzin and Chiappini 1994, Triapitsyn 1998, Williams and Martinson 2000). Triapitsyn (1998) considered *A. erythroneuræ* to be the most common egg parasitoid of the two major leafhopper pests of grapes in California and northern Mexico, which had likely been previously misidentified as *A. epos*. *A. erythroneuræ* parasitizes at least six genera and 16 species of leafhoppers, includ-

ing species attacking almond (*Prunus* spp.), apple, blackberry, table and wine grapes, prune (*Prunus* spp.), and willow (*Salix* spp.) (Triapitsyn 1998, Williams and Martinson 2000). This wasp species also has been reared from *Dikrella* eggs on blackberry and *T. pomaria* on apple (Triapitsyn 1998).

A. tretiakovæ was the most common mymarid reared from *Erythroneura* eggs in grape leaves; therefore, it may be an important regulatory agent of these pests in Washington vineyards. Triapitsyn (1998) reported that *A. tretiakovæ* primarily attacks *Erythroneura* spp. leafhoppers, including *E. ziczac* and *E. elegantula*, although parasitism of the latter has only been reported under laboratory conditions. Our study is the first to report field parasitism of *E. elegantula* by *A. tretiakovæ*. *A. tretiakovæ* also parasitizes at least three genera and nine species of leafhoppers on apple, table and wine grapes, and peach (*Prunus* spp.) (Williams and Martinson 2000); *Dikrella cockerellii* (Gillette) is also a likely host of this wasp species (Triapitsyn 1998).

Although agricultural practices can impact densities of many arthropods (Croft 1990; Prischmann et al. 2005a,b), with the exception of higher densities of *A. daanei* and parasitized *E. elegantula* eggs in non-managed sites in 2001, we did not find any effects of vineyard management on *Anagrus* densities. This likely reflects the fact that nonmanaged sites had higher densities of nonparasitized leafhopper eggs compared with managed sites that year. Additionally, because these parasitoids are highly mobile (Antolin

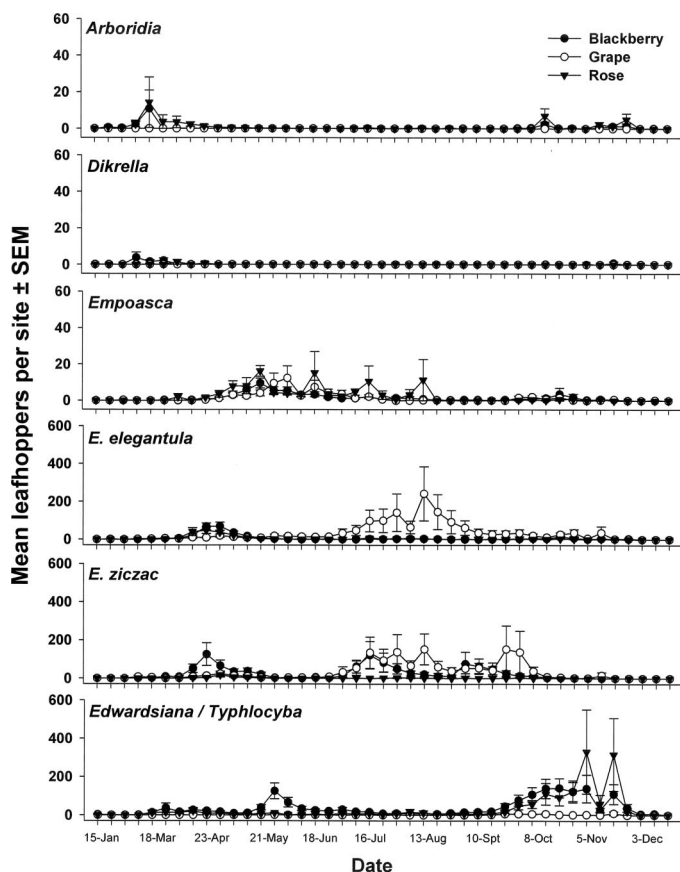


Fig. 5. Seasonal densities of leafhopper taxa collected from sticky traps in blackberry, grape, and wild rose habitats. The 2001–2003 data are combined. Data are means and standard errors.

and Strong 1987; Corbett and Rosenheim 1996a,b), they may emigrate from vineyards when conditions are unfavorable (i.e., after pesticide applications), and then return after conditions improve. Although some pesticides used in managed crops are harmful to these parasitoids, immature wasps might be partially protected as they develop within the host egg (Martinson et al. 2001). However, there were many differences between managed and nonmanaged sites other than pesticide input.

Management practices affected densities of leafhopper eggs, with higher densities of nonparasitized *E. elegantula* and *E. ziczac* eggs in nonmanaged sites. The major reason for this finding was probably the use of insecticides for leafhopper control in managed vineyards. James et al. (2002) found similar results for leafhopper nymphs in Washington wine grapes, as did Teulon and Penman (1986a) for adult typhlocybine leafhoppers (including *Typhlocyba froggatti* Baker) in New Zealand apple orchards. Canopy and plant characteristics can influence leafhopper densities, with higher leafhopper densities on shaded leaves (Cone et al. 1990, Trichilo et al. 1990, Wright et al. 1998), lower leafhopper densities on vines receiving less

water (Trichilo et al. 1990), and effects of variety on species composition (Martinson and Dennehy 1995). Some or all of these factors may contribute to the patterns in leafhopper densities that we observed.

We collected *A. atomus*, *A. daanei*, *A. erythroneuræ*, and *A. tretiakovæ* from traps associated with blackberry, grape, and wild rose plants, along with several potential leafhopper hosts. In addition, *A. atomus*, *A. erythroneuræ*, and *A. tretiakovæ* were the most common parasitoids emerging from blackberry and wild rose canes collected during winter (D. G. James and L. C. Wright, unpublished data). Because we did not rear *Anagrus* species from leafhopper eggs on these plants, we cannot make positive parasitoid–leafhopper–plant associations. However, *Anagrus* parasitoids often exhibit close density-dependent patterns with their leafhopper hosts (Seyedoleslami and Croft 1980, Teulon and Penman 1986b), and along with previously established associations, this study provides some evidence of potential relationships. *A. atomus* is known to parasitize leafhopper genera, including *Arboridia* (Hesami et al. 2004), *Empoasca* (de Courcy Williams and Gill 1996, Bünge et al. 2002), *Dikrella*, *Edwardsiana*, and *Typhlocyba* (Triapitisyn

Table 4. Statistical parameters for leafhoppers from sticky traps

	Wilks' λ	F	P
<i>Arboridia</i>			
Plant ^a	n/a	8.977	0.007
Yr ^b	0.981	0.077	0.926
Yr \times plant ^c	0.634	1.023	0.425
<i>Dikrella</i> ^d			
Plant ^a	n/a	1.695	0.237
Yr ^b			
Yr \times plant ^c			
<i>E. elegantula</i>			
Plant ^a	n/a	0.612	0.563
Yr ^b	0.514	3.781	0.070
Yr \times plant ^c	0.456	1.924	0.155
<i>E. ziczac</i>			
Plant ^a	n/a	1.199	0.346
Yr ^b	0.851	0.700	0.525
Yr \times plant ^c	0.536	1.463	0.260
<i>Empoasca</i>			
Plant ^a	n/a	0.813	0.474
Yr ^b	0.573	2.981	0.108
Yr \times plant ^c	0.487	1.733	0.192
<i>Edwardsiana/Typhlocyba</i>			
Plant ^a			
2001	n/a	14.445	0.002
2002	n/a	16.081	0.001
2003	n/a	18.233	0.001
Yr ^b	0.274	10.616	<0.001
Yr \times plant ^c	0.206	4.820	0.010

n/a, not applicable.
^a Univariate between subjects analysis: df = 2, 9.
^b Multivariate repeated measures analysis: df = 2, 8.
^c Multivariate repeated measures analysis: df = 4, 16.
^d No variation in dependent variable in repeated measures analysis.

1998), and it is likely that *A. atomus* parasitized one or all of these genera in our study. Unfortunately, *A. atomus* does not seem to parasitize *Erythroneura* spp. (Triapitsyn 1998) and thus is unlikely to be involved in suppression of grape leafhoppers in Washington vineyards. *A. erythroneurae* and *A. daanei* may have been associated with *Erythroneura* spp. on grape and *Edwardsiana/Typhlocyba* leafhoppers on blackberry and wild rose, whereas *A. tretiakovae* seemed to be associated with *E. elegantula* and/or *E. ziczac* on grape in the summer and fall.

Because grape leafhoppers overwinter as adults in plant debris near vineyards (Cone et al. 1990), the capture of significant numbers of *E. elegantula* and *E. ziczac* on sticky traps near blackberries in spring may represent their dispersal to alternate food plants before vineyard infestation (Wells and Cone 1989). The well-defined increase in captures of *Edwardsiana/Typhlocyba* in sticky traps during autumn likely represents the migration of *E. rosae* to *Rosa* and/or *Rubus* hosts for overwintering (Claridge and Wilson 1978). Dispersal of the first adult generation of *E. rosae* in spring also was indicated by sticky trap captures.

Several researchers have investigated how vegetation close to vineyards, including blackberry (Doutt and Nakata 1965, 1973; Williams 1984) and prune trees (Kido et al. 1984; Wilson et al. 1989; Pickett et al. 1990; Murphy et al. 1996, 1998), may enhance *Anagrus* densities and improve biological control of *Erythroneura* leafhoppers within a cropping system. English-Loeb et

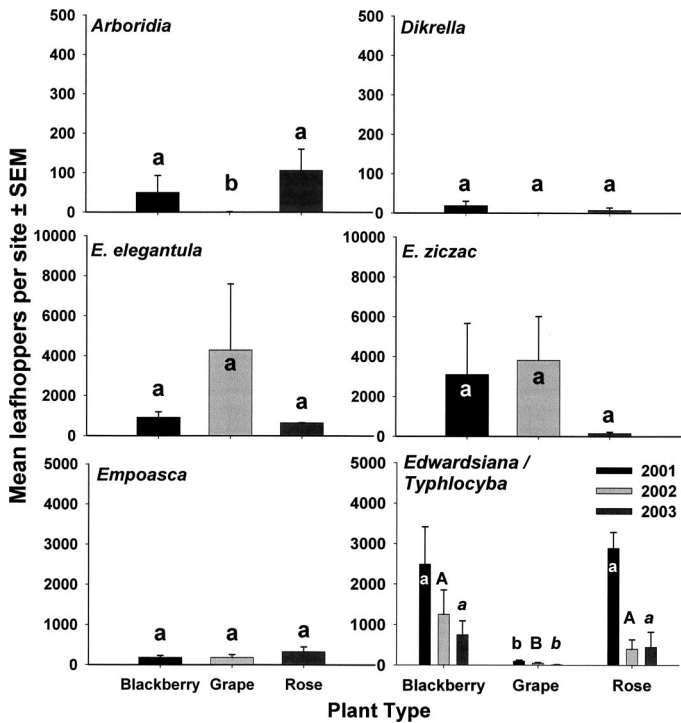


Fig. 6. Total densities of leafhopper taxa collected from sticky traps in blackberry, grape, and wild rose habitats. Data are means and standard errors.

al. (2003) found that interplanting nectar-producing cover crops enhanced *Anagrus* densities in New York vineyards. However, Letourneau (1990) and Nicholls et al. (2000) found that increasing plant diversity by using intercropping and a flowering cover crop, respectively, did not enhance densities of adult *Anagrus* or parasitized leafhopper eggs.

Like other parts of the United States, it seems that *Anagrus daanei*, *A. erythroneurae*, and *A. tretiakovae* are important biocontrol agents of *Erythroneura* leafhoppers in Washington state vineyards. From this study, it seems that *E. elegantula* may be better regulated by *Anagrus* spp. than *E. ziczac*, although the latter is equal or greater in abundance than *E. elegantula* (James et al. 2002). Therefore, improved egg parasitism of *E. ziczac* would likely reduce the overall impact of grape leafhoppers in Washington state vineyards. Furthermore, *A. daanei*, *A. erythroneurae*, *A. tretiakovae*, along with *A. atomus*, are associated with leafhoppers in blackberry and rose habitats, relationships that could potentially be exploited by these plants close to vineyards in an effort to enhance colonization by *Anagrus* species.

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